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Long-term monitoring of plant reproductive phenology and observation of general flowering in Lambir Hills, Sarawak

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Abstract General flowering (GF) is a community-wide masting phenomenon, which has thus far been documented only in aseasonal tropical forests in SE Asia. It is also one of the most spectacular and mysterious phenomena in tropical biology. GF occurs at irregular intervals of less than a year to several years. During such an event most dipterocarp trees and many other plants from shrubs to emergent trees to epiphytic orchids flower over roughly a three-month period. Conversely, flowers are scant between general flowering events. This type of community-wide masting has only been documented from this region. Since 1993, we have observed plant phenology from tree towers, walkways and a canopy crane in Lambir Hills National Park. We chose 486 individual plants of 300 species in 56 families to monitor phenology at the community level in 1993. The long-term monitoring of the forests have provided important clues for understanding the phenomenon. Proximate factors of general flowering have been the subject of controversy over the last decades. From the present observations, we concluded that drought was the most plausible trigger for general flowering. We have recorded a few large and many smaller general flowerings during the 20 years of observation. All flowering peaks were preceded by dry periods. The effects of such large fluctuations in flowering and fruiting intensities on population dynamics and host ranges of flower visitors and seed predators have been intensively investigated in Lambir Hills. Examinations in the field and laboratory have often revealed rather loose interactions, and great variations of population dynamics among taxonomic groups. Although many questions still remain to be answered, there is no doubt that general flowering has played a dominant role in structuring the hyper-diverse ecosystem of the dipterocarp forests.

Keywords Dipterocarp forests, General flowering, Mass flowering, Phenology, Plant reproductive ecology

Introduction

Bornean tropical rainforests have various unique characteristics such as high diversity of plants, dominance of the plant family Dipterocarpacese, and the height of the plants (Corlett and Primack 2011). One characteristic that should not be overlooked in terms of plant-animal interactions and regeneration of the forests is the peculiar plant reproductive phenology called general flowering (GF) (Sakai 2002). GF is a phenomenon of supra-annual mass flowering and fruiting at the community level. GF occurs at irregular intervals of less than a year to several years. During such an event most dipterocarp trees and many other plants from shrubs to emergent trees to epiphytic orchids flower over roughly a three-month period. Conversely, flowers are scant between general flowering events. The phenomenon is remarkable because most terrestrial communities from boreal to tropical communities have predominantly a one-year cycle in flowering phenology, although there may be small or large variations among years. Some communities may include a species or a closely related group of species that have a supra-annual flowering cycle and produce flowers only once in several years, but they are exceptions rather than the rule.

The GF phenomenon is also of importance in the management of forests and forest resources. In the richest forest of this region, the family Dipterocarpaceae may account for up to 10 % of all tree species and as many as 80 % of emergent individuals (Ashton et al. 1988). They are highly valued as a source of timber. Most dipterocarp species only flower during GF events, and thus GF is considered to play a key role in their reproduction. In addition, GF has broad repercussions on the life of local people, because supplies of some important forest resources are strongly associated with GF. Fruits of *Shorea* spp. (Dipterocarpaceae) called “illipe nuts” have been an important item of export. Statistics of the export of illipe nuts from Sarawak and Kalimantan show large fluctuations in the amount of the trade due to GF (Blicher-Mathiesen 1994). Other forest products, including wild fruits and the harvesting of honey from wild honeybees and catching of wild boars, the most popular animal for hunting, also change in association with GF. In spite of the scientific and economic and importance of the GF phenomenon, little scientific information was available about it until the 1980s.

One of the major goals of the Canopy Biology Program in Sarawak initiated in the early 1990s with the Lambir Hills National Park as the main field was to accumulate scientific knowledge about GF (Roubik et al. 2003). The project established a canopy observation system consisting of several tree towers and aerial walkways about 300 m long in total. A pillar of the canopy crane was later added as an observation platform. The late Tamji Inoue, who led the project, the late Kuniyasu Momose, who was a graduate student at that time, and many other researchers worked together and established a plant monitoring system using these towers and walkways. Thanks to many collaborators in Sarawak and Japan, the monitoring is still continuing, and it is recognized as one of the longest records of systematic field monitoring of plant phenology in the world. The purpose of this small article is to introduce the methodology of the monitoring and briefly summarise some of major achievements of the study.

Methods of the plant monitoring

Identification of the focal plants

To monitor plant reproductive activities in the forest, we have observed several hundreds of plants twice a month from terraces of the tree towers, walkways, and the pillar of the canopy crane (Roubik et al. 2005). One of the difficulties the founders of the monitoring system encountered was how to find and identify focal plants, because we could not reach the plants from the observation points on walkways and towers. Most focal trees had a tag on their tree trunk, but it could not be seen from the observation point. The founders used hand-drawn forest profile diagrams to record and identify the focal trees. A digital camera was not available yet at that time, and it took some time to develop photographs taken with a film camera. Soon the hand drawings were replaced by a series of photo books (Fig. 1) with a description of each plant. More recently, they have been fully digitized (Fig. 2).

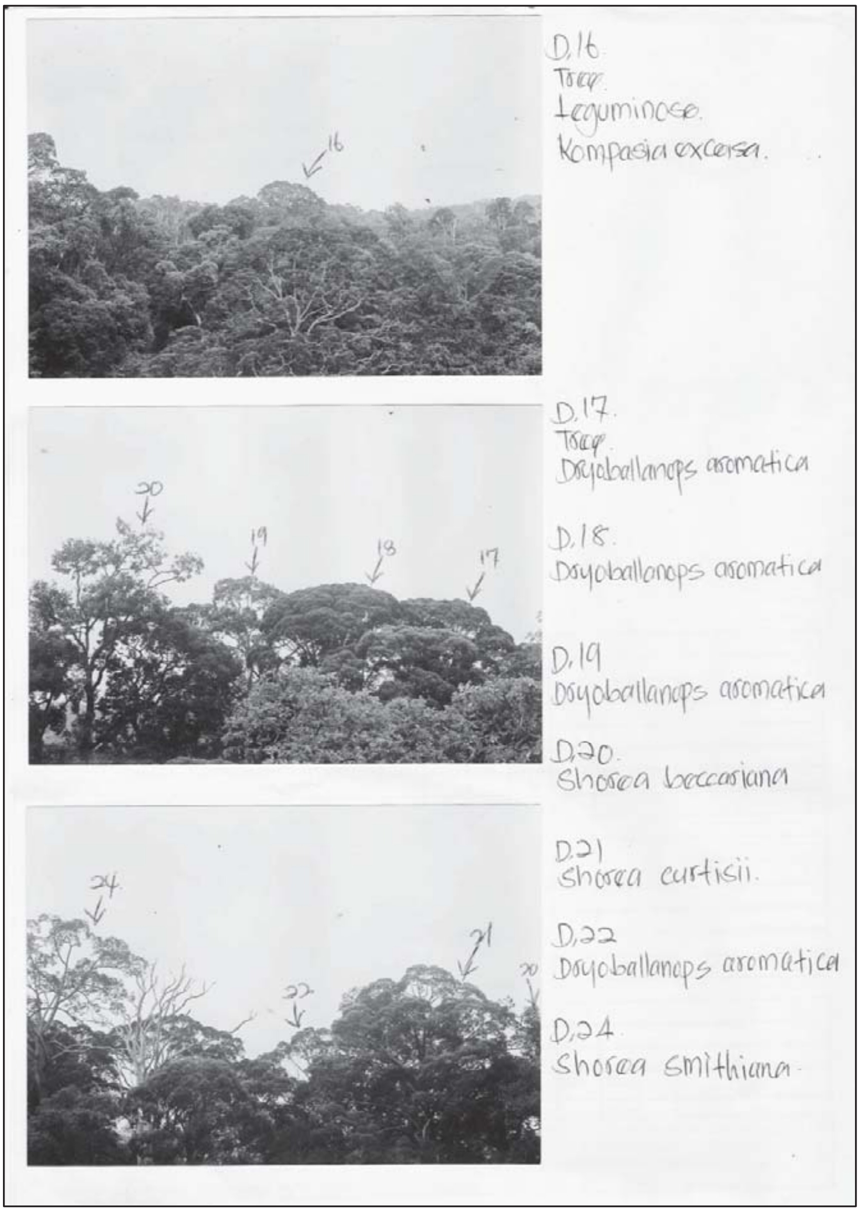

Fig. 1 A page of the previous photo book series used to identify plant individuals under the monitoring shown as an example.

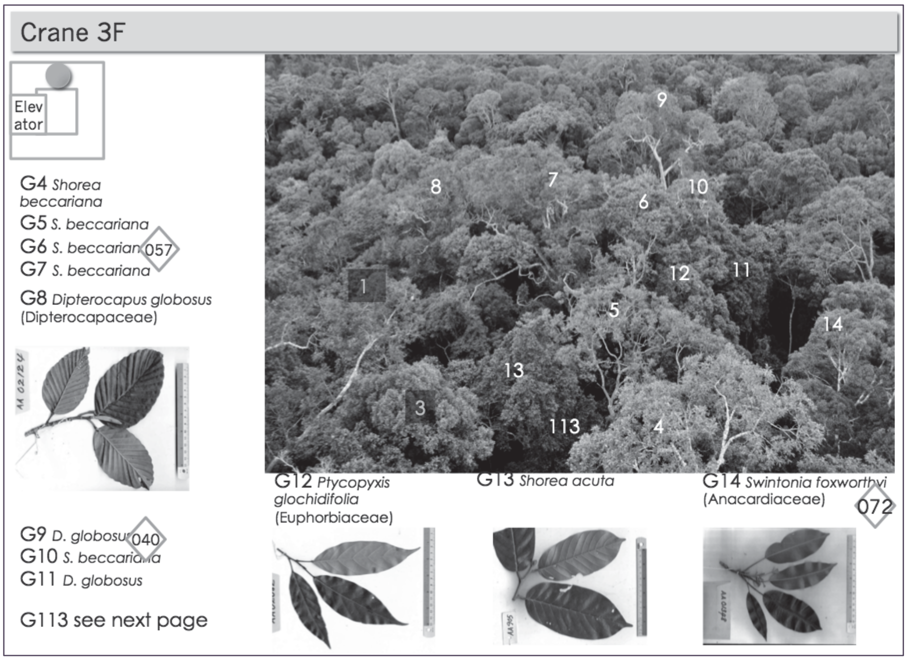

Fig. 2 A part of the digital file currently used to identify plant individuals under the monitoring shown as an example.

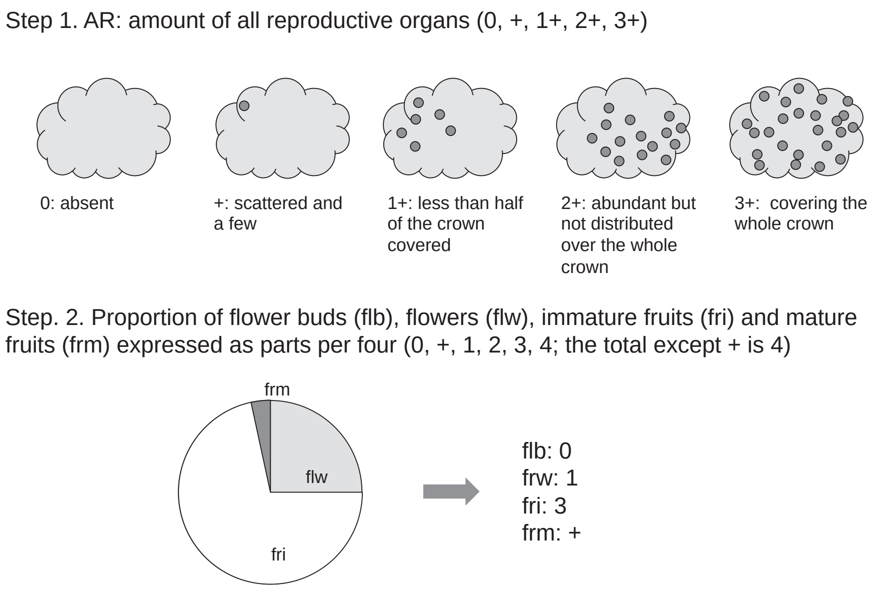

Fig. 3 Illustration of the method used to describe the reproductive status of the plants in the monitoring.

Description of the plant status

In the censuses, we describe the reproductive status of the focal plants ranging from emergent dipterocarp trees to epiphytic lianas using a common description method. We adopted a two-step

Amount of reproductive organs
Flowers
Immature fruits
Mature fruits

Year	Month	Day	ar	flb	flw	fri	frm	Note
2004	1	26	-					
2004	2	9	-					
2004	2	24	-					
2004	3	8	-					
2004	3	22	2+	4	0	0	0	
2004	3	30	2+	4	+	0	0	Reproduc. flushing.
2004	4	12	1+	1	2	1	0	Some flower disp.
2004	4	21	1+	0	0	4	0	
2004	5	10	1+	0	0	4	0	
2004	5	22	1+	0	0	4	+	
2004	6	11	1+	0	0	3	1	
2004	6	19	1+	0	0	3	1	
2004	7	1	1+	0	0	2	2	
2004	7	19	1+	0	0	1	3	
2004	8	2	+	0	0	0	4	Some fruit disp.
2004	8	16	-					
2004	9	1	-					
2004	9	20	-					Reproduc. no more.
2004	10	11	-					
2004	10	27	-					

Fig. 4 An example of a reproductive event from flower bud appearance to fruit dispersal captured by periodical observations described by the method illustrated in Fig. 3. This example shows a reproductive event of *Dryobalanops lanceolata* (Dipterocarpaceae) of Tower 1.

evaluation system (Sakai et al. 1999) (Fig. 3). The first step is the description of the total amount of all reproductive organs, namely mature and immature flowers and fruits, using five grades. If the plant does not have flowers or fruits, the grade is 0. When it has some flowers or fruits but the number is very small compared with the size of the plant, the grade is +. If flowers and fruits are abundant enough to cover some portion of the plant crown, but cover less than half of the crown, the grade is 1+. If flowers or fruits are abundant enough to cover more than half of the crown but not the whole crown, the grade is 2+. If flowers and fruits cover the whole crown, the grade is 3+. The second step is the description of the proportion of flower buds (flb), flowers (flw), immature fruits (fri) and mature fruits (frm) among the reproductive organs expressed as parts per four (0, +, 1, 2, 3, 4; the total except + is 4).

A typical example of a record of a reproductive event is shown in Fig. 4. This record describes a reproductive event of Tree tower 1 in the 8-ha plot in 2004. The observer found flower buds on March 22nd, and recorded flowering in the following census. Flowers developed into fruits and matured in June and July, and all fruits had been dispersed before the middle of August.

Turnover of the plants under observation

The monitoring was started in 1993; at this point the censuses were conducted in the Canopy Biology Plot and along the waterfall trail for tourists. In total, 486 plants of 300 species in 56 families were in the list of the plants under observation. Among the plants, 430 were observed from the towers and walkways in the 8-ha Canopy Biology Plot established by the Canopy Biology Program in Sarawak, and 56 plants were observed using the Operation Raleigh Tower along the waterfall trail, which was a tree tower constructed as a tourist attraction by Operation Raleigh and donated to the park (Sakai et al. 1999).

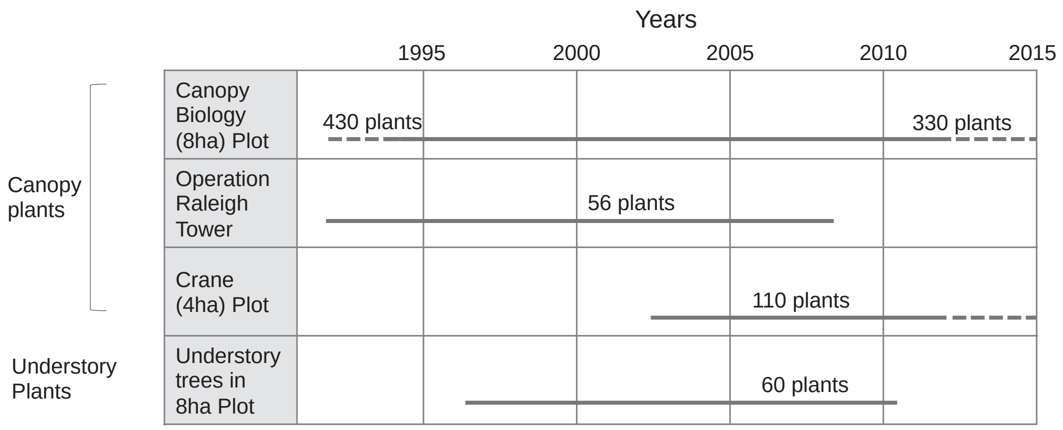

Fig. 5 Turnover of the plant under the observation. Part of the results for the canopy plants have been published in Sakai et al. (1999) and Sakai et al. (2006), while those for the understory plants are still unpublished.

During the long-term monitoring, some of plants were removed from or added to the list of the focal plants (Fig. 5). The observation of the Operation Raleigh Tower was stopped due to deterioration and removal of the tower. After the construction of the crane, we added about 100 plants in the 4-ha Crane Plot to the list. In addition, we have made small changes of the list time to time due to deaths of plants and changes in the route of walkways. Thanks to the great contributions of the staff of the Forest Department, observation of plants in the 8-ha Plot and 4-ha Plot is still continuing.

In addition to these plants observed from the towers, walkways and the crane, we monitored 60 understory plants along a trail in the 8-ha Plot. This monitoring was stopped in 2011.

Major achievements

Description of GF

We observed the first GF event in 1996 (Sakai et al. 1999) (Fig. 6). During the first few years of the monitoring, the proportions of flowering and fruiting plants were very low, 2–5 %. In other words, we recorded “0”s for most of the plants in every census twice a month. In 1996, we observed a sharp increase in the proportions of flowering and fruiting up to 17 % and 25 %, respectively. Interestingly, we observed two flowering peaks in this year. During the GF, many plant species that had not flowered yet massively produced flowers and fruits. Some plants flowered in both flowering peaks. Figure 7 shows the flowering periods of different plants of various families. It illustrates that the flowering periods of these species were significantly staggered, although flowering was concentrated in the period from March to May (Roubik et al. 2005). One of our major findings in this GF was that plants of diverse taxonomic groups joined GF. Sakai et al. (1999) categorized the plants into five groups depending on the flowering patterns from 1993 to 1996. Plants that flowered only during GF period were classified into the GF type. The results showed that not only dipterocarp species but also other plant groups such as Euphorbiaceae, Leguminaceae, and even some orchids were included in the GF type. This confirmed that GF was a phenomenon of the whole plant community rather than masting of a single plant group.

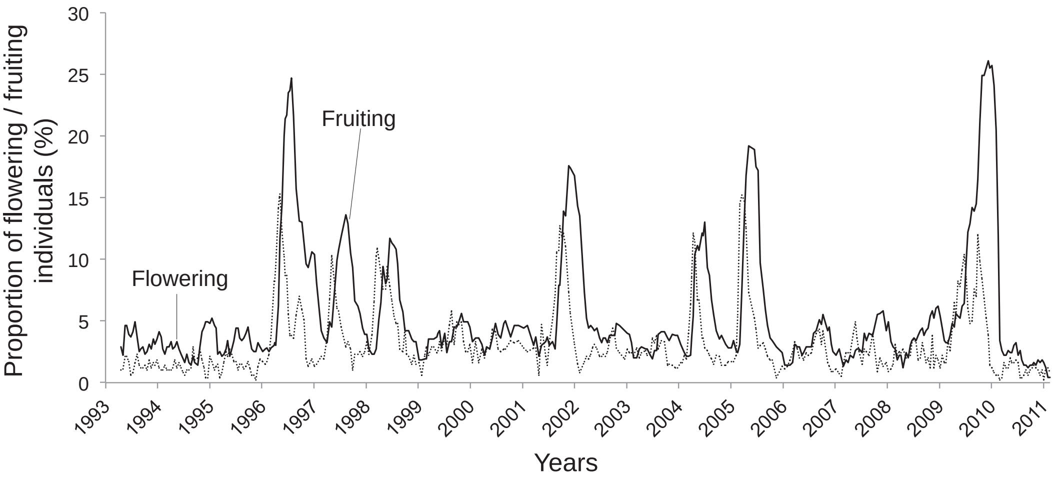

Fig. 6 Changes in the proportions (%) of flowering (dotted line) and fruiting (solid line) individuals among the canopy plants (see Fig. 5) during the monitoring. Fruiting peaks are generally higher than flowering peaks, because the period of fruiting is usually longer, and overlaps of the fruiting periods among individuals are more extensive than those of flowering. Sakai et al. (unpublished data).

Response of animals to GF

After the GF in 1996, we observed GFs in 1997 and 1998 (Fig. 6); Repeated GF events provided researchers with valuable opportunities to assess the responses of various mammals and insects to GF. One of the insects that showed drastic response to GF was giant honeybees (*Apis dorsata*, Hymenoptera). These bees have great mobility and migrate flexibly depending on the resource availability of the habitat. Monitoring of the population of giant honeybees in the 8-ha Plot using regular light trap censuses clearly showed great fluctuations in number, which tracked the flowering activities in the forest (Itioka et al. 2001). Some species of GF plants depend on giant honeybees for pollination (Momose et al. 1998). Synchronized flowering among species may enhance animal pollination by inducing immigration of migratory pollinators (Sakai 2002).

The response of animals depending on plant reproductive organs, however, varies among taxonomic groups and species. Based on live-trapping data, Nakagawa et al. (Nakagawa et al. 2007) showed that the abundance of small mammals increased and peaked after 3-4 months after a fruit fall, when seedlings had already been established. Therefore, they suggested that supra-annual fruiting of GF satiated predation by small mammals and reduced mortality of seeds and seedlings. On the other hand, Kishimoto-Yamada et al. (Kishimoto-Yamada et al. 2009) reported considerable variation in the population dynamics among light-attracted chrysomelid beetles (Chrysomelidae, Coleoptera). Some of these beetles are reported to be pollinators of *Shorea* spp (Dipterocarpaceae) in Lambir (Momose et al. 1998). They investigated population fluctuations of the 34 most dominant species, and found little association with GF. Instead, the beetles showed stronger responses to a severe drought in 1998. One of the potential reasons for the weak association with GF is the wide host-range of these beetles (Kishimoto-Yamada et al. 2013).

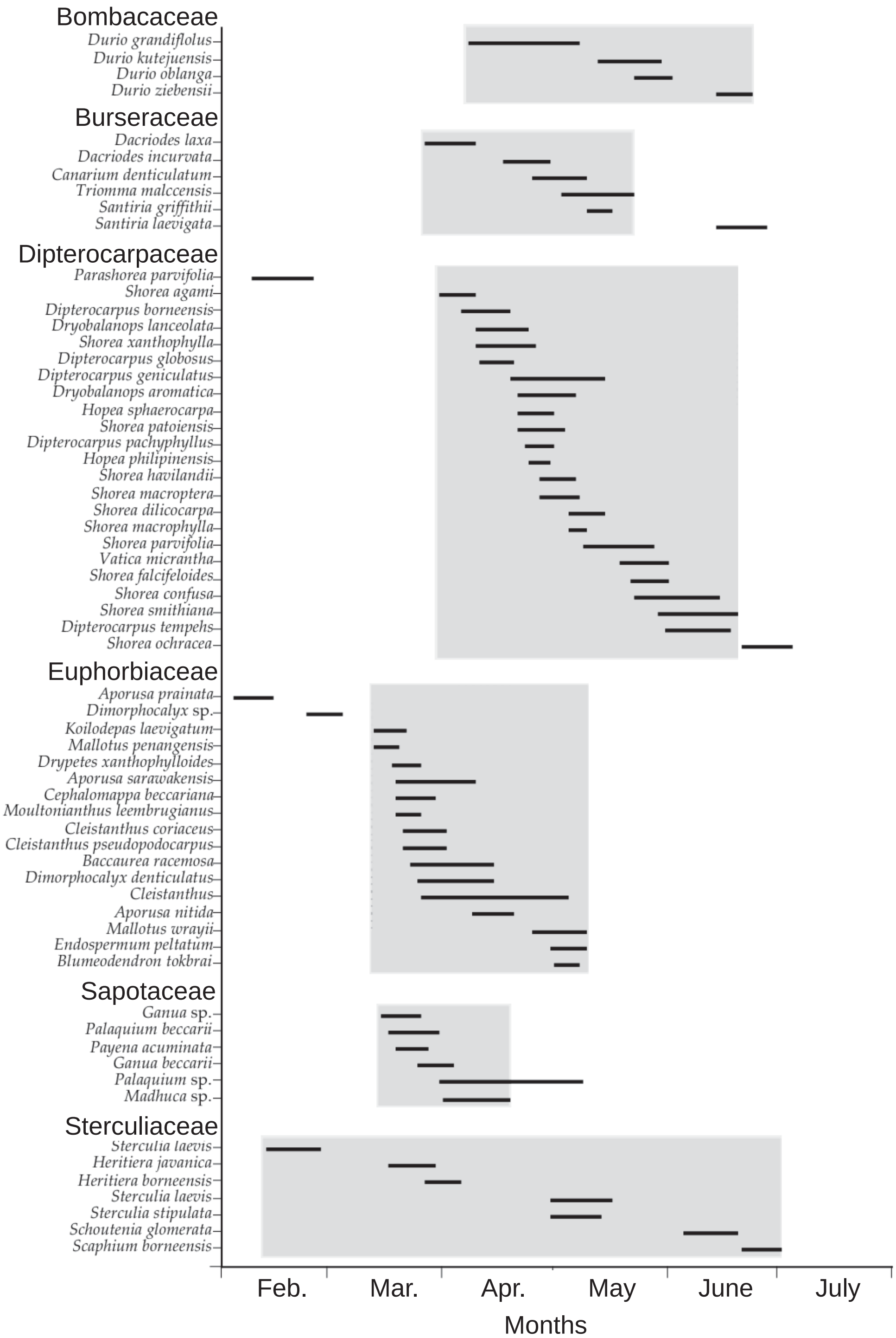

Fig. 7 Flowering periods of different taxonomic groups during the 1996 GF. Modified from Roubik et al. (2005).

Trigger of GF

Prior to our study, an influential paper on GF (Ashton et al. 1988) had examined proximate factors for GF. Specifically, the paper closely investigated temperature and flowering data from Pasoh

Forest Reserve in Peninsular Malaysia. It concluded that temperature drop was the most plausible trigger for GF. In the GF of 1996, supporting this hypothesis, we found a sharp drop of temperature just before flowering. Therefore, we regarded it as the trigger in the paper describing the GF in 1996 (Sakai et al. 1999). However, after additional observations during several years, we found that some flowering events occurred without a preceding temperature drop. This motivated us to take a second look at this issue.

In the second investigation, we found that droughts, or relatively short dry spells, were more likely triggers than temperature drops, at least in our forest (Sakai et al. 2006). We found a stronger association between flowering and 30-day running total precipitation than between flowering and temperature drops. We overlooked this association in the previous analysis partly because we used monthly precipitation rather than running total precipitation.

It is still an unsettled question, however, if GF in every location is always triggered by a drought. A few research groups have published results consistent with our conclusion (Brearley et al. 2007, Cannon et al. 2007), but there have also been suggestions that temperature drops also significantly contribute to determine the timing of the phenomenon (Yasuda et al. 1999).

Concluding remarks

The long-term monitoring of plant reproductive phenology has significantly contributed to the accumulation of scientific knowledge about GF in this region. Although many questions still remain to be answered, there is no doubt that GF has played a dominant role in structuring the hyper-diverse ecosystem of the dipterocarp forests. Environments in Bornean tropical rain forests are considered to be subject to the effects of global and local climate changes (Kumagai and Porporato 2012). Further studies of GF are essential for better understanding and conservation of this valuable ecosystem.

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